Management by proxy? The use of indices in applied ecology

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Journal of Applied Ecology encourages contributions that can influence environmental management, policy or both, with evidence based on the most robust science possible. Natural resource management is often contentious, and any perceived weaknesses in the underpinning science are easily exploited by interest groups to undermine the wider endeavour (see, e.g. the experiences of the Intergovernmental Panel on Climate Change, Ravindranath 2010). Thus, the robustness of science designed to underpin management and policy is particularly important.

Unfortunately, robust and unambiguous results are difficult to obtain in ecology. In particular, causal pathways in ecology are seldom linear, but are part of a 'vast web of cause and effect' of which, typically, we can study only a small part (Peters 1991; p. 134). Meaningful spatial and temporal scales for ecological processes often defy experiments, controlled manipulations and adequate replication; most modern ecological science is reliant on observational data and correlation is far easier to demonstrate than causation (cf. Sugihara et al. 2012). Formal experimentation is clearly impossible in the context of many of the most pressing questions of societal relevance, such as those regarding the impacts of climate change, large-scale agricultural intensification and habitat loss. The conceptual frameworks that inform our understanding of these processes often rely on entities that can be hard to measure directly and, thus, ecologists often depend on proxies or surrogates for those entities. In natural resource management, for example, common proxies include measures assumed to capture the conservation status of species, as well as measures assumed to provide information on ecosystems' distribution, structure, functioning and service delivery (Mace et al. 2008; Ayanu et al. 2012; Pettorelli et al. 2014).

Several studies have already pointed out issues and pitfalls related to the use of proxies in ecology and evolution (see, e.g. Nieberding & Olivieri 2007; Sekar 2012; Best & Stachowicz 2013) but less consideration has been given to the impacts of proxies on the robustness of management recommendations at a range of scales (but see Eigenbrod et al. 2010). This is despite the fact that proxies are a vital part of an applied ecologist's toolkit and are frequently used to link science with management and policy (Turnhout, Hisschemo€ller & Eijsackers 2007). Here, we discuss the role of proxies in applied ecology and management by examining three recent examples of problematic issues: proxies for the abundance of animal populations; proxies for habitat quality; and proxies for ecosystem functions and ecosystem services delivery. While this list is far from exhaustive, these are issues we frequently see as journal editors. They provide a useful starting point to discuss possible directions to improve our use of proxies in natural resource management.

Proxy-based measures of population abundance

Population size is a key requirement for supporting local decision-making in species-based management and is also used to inform several national and international policies and regulations. For example, population size and the rate at which it changes are fundamental to species listing and delisting decisions under the Endangered Species Act (U.S. Senate Committee on Environment & Public Works 1973) and for the IUCN Red List (Mace et al. 2008); these decisions have knock-on implications for the international trade of organisms (CITES 1973).

The use of indices as proxies for population abundance is perhaps one of the most widely recognized areas of contention in applied ecology. Across vast geographic areas, the relative abundances of many wildlife populations of cultural or economic importance are assessed using surveys that yield indices, rather than estimates, of abundance (Schwarz & Seber 1999). These include, for example, track counts used to monitor the abundance of many mammal species, camera trapping rates used to index the abundance of elusive or low-density species, pitfall traps to assess invertebrate populations, and hunting offtake used as an index of the abundance of many game birds and mammals. These proxy methods have all been the focus of considerable concern (McDonald & Harris 1999; Jennelle, Runge & MacKenzie 2002; Pollock et al. 2002; Webbon, Baker & Harris 2004; Keane, Jones & Milner-Gulland 2011; Saska et al. 2013). The central criticism relates to the generally unverified assumption that the relationship between the index and the true abundance is direct and constant (Pollock et al. 2002). One basic issue underpinning this criticism is that all of these methods depend on encounters (between observers, cameras, traps or hunters and tracks, animals or quarry) which, in turn, depend on the levels of activity of individuals of the focal populations, the detectability of their signs and the extent of efforts to locate them. These factors are not expected to be static in either space or time (Pollock et al. 2002) and could be affected by behavioural changes along ecological gradients of management interest (such as agricultural intensification).

In spite of these criticisms, indices of abundance remain in widespread use for a combination of reasons. First, collecting indices tends to be a lower-cost approach than determining absolute estimates of abundance (Jones 2011). Second, as Caughley (1977)

observed, ‘absolute estimates of density [are often] unnecessary luxuries’, and management practices such as threshold harvesting or studies of relative habitat utilization are not reliant on estimates of absolute abundance. Third, in some situations, evidence suggests that indices can provide a reasonable proxy for abundance. A recent applied example relates to a critical issue in Australian wildlife management. Specifically, the extent to which track counts reflect true abundance is a key concern about studies of the ecological impacts of the dingo Canis lupus dingo (Hayward & Marlow 2014). In defence of those studies, Nimmo et al. (2015) cite work showing that track counts were linearly related to the true abundances of various carnivores in a number of specific studies. Moreover, they point out that, for elusive species, indices based on abundant field signs might well be associated with lower uncertainty than population estimates based on sporadic but infrequent direct sightings (Nimmo et al. 2015).

In summary, proxies for population abundance are widely used and often criticized. They might be adequate in some situations but that will usually depend on the specific management question being addressed. More often, indices of abundance are vulnerable to criticism and will require careful calibration.

Proxy-based measures of habitat quality

Identifying potential sites suitable for species translocations, or sites at which we should prioritize restoration efforts, are important management activities world-wide. Habitat monitoring is also strongly encouraged by international conventions: the Convention on the conservation of migratory species (CMS), for example, explicitly states that ‘parties that are range states of a migratory species shall endeavour to conserve and, where feasible and appropriate, restore those habitats of the species which are of importance in removing the species from danger of extinction’ (www.cms.int).

Habitat is usually defined as the resources and conditions present in an area that produce occupancy – including survival and reproduction – by a given organism (Morrison, Marcot & Mannan 1992). The spatial extent and resolution at which habitat is defined tends to be a function of several variables, such as the number of individuals considered, the body size of the species considered, and the spatial resolution at which habitat selection patterns are explored (itself shaped by the availability of environmental and species occurrence data; Pettorelli 2013a,b).

Within this context, habitat quality is sometimes perceived as some function of fitness or per-capita population growth (Van Horne 1983; Johnson 2007), where these are expected to be higher in high-quality habitats. The problem with this definition of habitat quality is that measuring per-capita contributions to population growth in a given habitat requires intensive monitoring, usually over a long period. As a result, attempts to capture variation in per-capita population growth often use information that is less costly and time consuming to obtain, such as abundance, survival, body condition or corticosterone levels of the focal species (see, e.g. Van Horne 1983; Marra & Holberton 1998; Johnson 2007).

It has also been assumed that habitat suitability, usually determined from occurrence or presence/absence data using species distribution models (SDMs), will provide a useful indication of habitat quality (see, e.g. Larson et al. 2004; Martin et al. 2012). Working with the giant kangaroo rat Dipodomys ingens, Bean et al. (2014) compared these different proxies for habitat quality, using SDMs generated at a range of scales. They found that habitat suitability from SDMs correlated with abundance (especially when SDMs were parameterized at a fine scale) but not with survival or body condition. Life-history theory is reassuring in this regard, providing good reasons why neither survival (Pilastro, Tavecchia & Marin 2003) nor body condition (Houston & McNamara 1993) need be strongly related to habitat quality. More troubling, however, is that ecology also provides reasons to question the relationship between population abundance and habitat quality, especially where despotic behavioural processes can result in large numbers of individuals being excluded from high-quality (and into marginal) habitats (Van Horne 1983). These considerations call into question a number of widely used proxies for habitat quality.

Habitat quality is unquestionably related to the availability of resources, but also to levels of predation. Which of these predominates in determining the quality of habitat for a given population is often described using the terminology of ‘bottom-up’ vs. ‘top-down’ control (e.g. Hunter & Price 1992). The proportion of mortality attributable to predation is sometimes used as a proxy for the extent of top-down control (Sinclair, Mduma & Brashares 2003; Hopcraft, Olff & Sinclair 2010). Paradoxically, however, behavioural modelling of risk-sensitive foraging shows that an increase in predation may well result from a decline in food availability (McNamara & Houston 1987). These results appear to be borne out in empirical systems (Sinclair & Arcese 1995), undermining the use of predation rate as an index of top-down control and emphasizing the difficulty of teasing apart these processes.

Overall, theoretical considerations suggest that proxies for habitat quality and the processes that determine it will often be flawed. As with proxies for abundance, however, proxies for habitat quality might be suitable for addressing management questions at some spatial scales. The challenge remains to identify those situations under which proxies are useful and to determine alternative approaches where they cannot be used.

Proxy-based measures of ecosystem function and service delivery

With a policy agenda increasingly focused on ecosystem service provision (Perrings et al. 2010), understanding the ecology of ecosystem functioning and its implications for the delivery of ecosystem services has never been more important.

It can be extremely difficult to measure ecosystem function or service directly, and spatial proxies, such as smallscale above-ground biomass in plants, are often employed (e.g. Tilman et al. 2001). Perhaps less widely appreciated, however, is the fact that certain easily measured ecosystem functions are sometimes used as proxies for more difficult to measure ecosystem functions and services. For example, most biodiversity–ecosystem function experiments measure productivity and assume that this parameter correlates with a broader suite of ecosystem functions and services. Yet recent work has shown that

ecosystem productivity can be quite divergent from functions and services such as methane consumption, pest control and pollination (Werling et al. 2014).

A vast array of approaches to measure ecosystem functions and/or ecosystem services is currently available to ecologists and managers. Large-scale attempts to assess ecosystem productivity might rely on proxies such as climatic and structural variables that correlate with productivity (Ruiz-Benito et al. 2014), or vegetation indices derived from remote sensing information (Pettorelli 2013b). Identifying which methodological approaches and proxies are likely to support robust decision-making in a given context is a particular challenge. The European Union's Water Framework Directive (WFD), for example, uses an ecological status score for aquatic habitats to represent the amount of ecosystem service provisioned. One recent assessment of the WFD's use of ecological status

found that status correlates with some ecosystem services and taxonomic diversity (Tolonen et al. 2014), suggesting that this proxy is useful for quickly assessing overall service delivery (though caution is required when considering single or few services). By contrast, recent analyses have shown that land cover type (e.g. Ayanu et al. 2012) is a poor proxy for ecosystem service, with potential to mislead management strategies (Eigenbrod et al. 2010).

Species-based proxies for assessing ecosystem function and service delivery have also been heavily discussed. Two decades of research have now been devoted to testing the hypotheses that higher species diversity leads to greater ecosystem function and service delivery, with the view to establishing species richness as a proxy for these ecosystem attributes (Balvanera et al. 2006; Cardinale et al. 2006). Results so far, however, seem to indicate that functional diversity (Petchey & Gaston 2006; Mouchet et al. 2010; Cadotte, Carscadden & Mirotchnick 2011), rather than species richness itself, directly affects ecosystem function and the delivery of ecosystem services (Tilman et al. 2001; Cadotte, Carscadden & Mirotchnick 2011; Woodcock et al. 2014). Species loss may be functionally random, with the result that certain extinction scenarios may have minimal effects on functional diversity (Sasaki et al. 2014), rendering species loss an unreliable indicator of ecosystem function loss. Interestingly, both functional and phylogenetic diversity have actually been shown to explain variation in ecosystem function (Flynn et al. 2011; Cadotte 2013). However, there are cases where phylogenetic and functional diversity may not be strongly correlated and actually show different responses to disturbance or management (Cadotte, Albert & Walker 2013; B€assler et al. 2014). Clearly, more work is required to understand how well these facets of diversity correspond to the important ecological differences that influence the ecosystem functions that may attract management interventions.

Overall, the validity of different proxies for ecosystem function and service provision has been the focus of much research but few proxies have been shown to work well across a wide range of scenarios. Proxies should be used cautiously in situations in which they have been shown to work, or subjected to further validation beyond those circumstances.

Where should we go from here?

The examples above highlight the challenges of drawing robust management-relevant inferences from ecological science, providing insights into the appropriate use of proxies and ways to move forward. Here, we suggest three essential considerations when using and/or developing proxies.

THE CORRECT USE OF PROXIES DEPENDS ON BOTH AIMS AND SCALES

As with so much in ecology, the relevance of proxies often depends on the scale of enquiry. As illustrated by Bean et al. (2014), spatial resolution and spatial extent are correlated entities in most habitat quality assessments. Unsurprisingly, assessments focused on smaller areas or utilizing environmental data collected at greater spatial resolution are capable of detecting greater variability in apparent quality than coarser, large-scale studies. Extent and resolution are, thus, important parameters that directly shape the usefulness of habitat quality assessments: broad-scale models are more likely to be adequate for identifying potential protected areas, whilst finer-scale models will be required to inform local management strategies such as habitat restoration.

Spatial scale is also likely to be fundamental to debates about the usefulness of prey availability as an indicator of habitat quality for predators. Recent work on the sublethal effects of predation and the 'landscape of fear', shows that prey will often be most abundant in areas in which they are relatively inaccessible to predators and, thus, that the correlation between prey abundance and prey availability may be low (Laundr□e 2010). This suggests that, at a fine scale, prey availability might be a poor proxy for habitat quality – but, at a landscape scale, predators will still prefer areas with abundant prey. Thus, the spatial scale at which a question is posed has a strong bearing on the relevance of a given proxy.

Temporal scale might also shape the relevance of a proxy. Owing to variation in activity among years, proxies for population density based on either sighting rates or spoor abundance might be poor indicators of interannual changes in population size. However, unless activity or detectability show long-term, deterministic trends, such indices will be useful to identify the existence of trends in abundance over longer time frames. Even over short time frames, indices might be useful, as long as the variation in detectability and activity is independent of abundance and of substantially lower magnitude than the variation in population size that researchers wish to detect (Johnson 2008). Whether or not this is the case should be a focus of work aimed at validating these proxies.

All studies face logistical and financial constraints, which create an immediate tension between spatial replication and improving the resolution of temporal information. While the recent use of occupancy and detectability models encourages improved temporal resolution, this can come at a cost of understanding important spatial drivers of species distributions which, in many cases, may be more important from a conservation perspective (BanksLeite et al. 2014).

Confidence in a given proxy is directly related to the amount of evidence validating its use. Proxies tend to be sensitive to local conditions, so calibration is often a requirement of validation. Validating various proxies for

population abundance has been the focus of significant effort. As discussed above, Nimmo et al. (2015) presented a range of evidence to support the use of track abundance as a useful proxy for abundance of medium to large carnivores. Of course, this does not mean that track abundance will be a useful proxy in all situations. Other work has focused on calibrating indices of abundance and controlling for factors that determine how the relationship between the index and actual abundance varies across time and space. For example, Stephens et al. (2006) analysed GPS data on movement of ungulates in the Russian Far East to identify factors that affect daily travel distances. In this way, they were able to adjust for time of year (where relevant) when relating index values to absolute abundances. Similarly, Saska et al. (2013) assessed the impact of temperature on the activity of invertebrates, thereby allowing them to control for activity when relating pitfall trapping success to relative abundance. Adjusting for activity or travel distances can also facilitate comparisons of abundance indices across species, whether those indices are based on track counts (Keeping 2014) or photographic trapping rates (Rowcliffe et al. 2008; Rovero et al. 2009). Methods are also available for controlling for sources of bias when using indices of population density based on faecal abundance. Specifically, Jenkins & Manly (2008) recommended approaches for controlling for inaccuracies arising from both observational bias and faecal decay rates, both of which can undermine the use of faecal counts as proxies for abundance.

Reviews assessing the validity of various proxies of habitat quality are also accumulating (see, e.g. Johnson 2007; Pettorelli 2013b). Support for proxies of habitat quality derived from habitat suitability modelling can be found in work that seeks, retrospectively, to predict the quality of recolonized habitat. This approach, used by Cianfrani et al. (2010) for assessing the spread of otters Lutra lutra, showed that habitat suitability modelling can predict recolonization areas well, implying that these models do produce useful proxies for habitat quality (although that finding is sensitive to the method used). One caveat to this is that habitat suitability modelling based on presence-only or presence/absence data cannot discriminate between source and sink habitats. Consequently, Falcucci et al. (2009) recommend incorporating measures of demographic performance into habitat suitability models; inevitably, however, those measures will themselves often be proxies for performance.

As discussed above, proxies for ecosystem function and service provision have also been subjected to extensive validation, but with varying results. Although several proxies have increasing support, ecosystem service provision, in particular, describes a wide array of processes (Millennium Ecosystem Assessment 2005). Thus, further validation is likely to be required to show that supported proxies apply well across contexts.

One of the fundamental requirements for proxies emerges from the limited spatial and temporal scale of most ecological work. However, new technologies and larger-scale research programmes can help to calibrate and validate proxies and might also reduce our reliance on them. The USA's National Earth Observatory Network (NEON; http://www.neoninc.org), for example, is a large-scale programme, which will combine ground-based information on biodiversity distribution with remotely sensed data. The programme is set to run over decades at an established network of sites and therefore has the potential to provide direct measurements of the link between biodiversity and ecosystem services, thereby helping to calibrate our understanding of this relationship. Elsewhere, Brazil also promotes long-term ecological research, with a network of 30 sites across the country (PELD; http://www. cnpq.br/web/guest/apresentacao7). Other programmes are emerging on even grander scales. The International Cooperation for Animal Research Using Space (ICARUS; http://icarusinitiative.org) programme will include animal monitoring instrumentation on board a research module of the International Space Station. This will enable remote monitoring of the movements and fates of large numbers of individuals of species far smaller than can be remotely tracked at present. Among many advantages, this will allow direct measurements of habitat use and the consequences of habitat selection, on a scale beyond anything currently possible, thereby improving our understanding of the validity of proxies for habitat quality.

Applied ecologists should continue to make the case that natural resource management and environmental policy demand the strongest possible underpinning science. Despite the lower academic appeal of monitoring work, robust approaches to policy and management often require detailed, long-term monitoring, enabling us to document key ecological phenomena on a scale that obviates the need for proxies. As Martin Wikelski, head of the ICARUS programme has observed: we take it for granted that governments will cooperate to provide vast funds to look for life on other planets – but we still know very little about the one planet where we already know that life exists. Ecologists must not be shy about demanding funding for large, long-term monitoring projects that yield real insights into the key ecological processes supporting life on Planet Earth. Such insights could radically transform our understanding of ecological systems and, thereby, the ability of managers and policymakers to reconcile biodiversity maintenance with human well-being.

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